Predator–prey relationships in a changing environment: the case of the sparrowhawk and its avian prey community in a rural area

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Summary

1. Changes in community composition are expected to entail cascading effects at different trophic levels within a food web. However, empirical evidence on the impact of changes in prey communities on the population dynamics of generalist predators, and on the extent of possible feedback processes, remains scarce.

2. We analysed the dynamics of a generalist predator, the European sparrowhawk *Accipiter nisus* L., in a rural area of Northern Denmark. Over a 20-year period, the diet of the predator has been thoroughly assessed (> 30 000 identified prey items) and quantitative information about its avian prey community, based on standard breeding bird surveys, has revealed significant trends for several passerine species, although the overall prey biomass available remained stable.

3. The growth rate of the sparrowhawk breeding population was negatively related to the previous sparrowhawk density and to winter temperature, but was positively related to available prey biomass. Contrary to expectations for a generalist predator, sparrowhawks seemed to be predominantly sensitive to changes in the cumulative abundance of their two main prey species, the skylark *Alauda arvensis* L. and the blackbird *Turdus merula* L., but less so to changes in the wider prey community.

4. In demographic terms, the two-phase sparrowhawk dynamic recorded here (a recovery following an initial decrease) was mainly driven by recruitment of yearling females into the breeding population rather than by variation in the apparent survival of breeding females.

5. Our findings emphasize that changes in the composition of a prey community, affected by environmental changes, impacted population dynamics of a generalist predator. Finally, we found conditions that might enable apparent competition between blackbirds and song thrushes *Turdus philomelos* L. to occur. High blackbird abundance, maintaining sparrowhawks at a relatively high density may, in turn, push song thrushes into a predator pit.

Key-words: *Accipiter nisus,* demography, generalist predation, global change, growth rate, predator pit, prey community

Introduction

Much progress has recently been achieved in investigating the link between environmental variation and processes underlying population dynamics (Lande, Engen & Sæther 2003; Coulson, Rohani & Pascual 2004). In most species, availability of food resources has been identified as the key factor that influences reproductive output (Brommer, Pietiäi-

nen & Kolunen 2002), survival (Ruf *et al.* 2006), recruitment (Rutz & Bijlsma 2006) and, ultimately, the growth rate of the population (Sinclair & Krebs 2003). This is especially apparent for predator species situated at the top of trophic networks.

There are, however, few studies that base their conclusions upon direct measurements of variation in food resources. Instead, studies use surrogates such as weather conditions or population density to characterize food conditions (Dennis & Otten 2000; Coulson *et al.* 2001), or focus on systems

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involving trophic interactions between a specialist predator and one or a few main prey species (Korpimäki & Norrdahl 1991; Angerbjörn, Tannerfeldt & Erlinge 1999; Nielsen 1999; Vucetich, Peterson & Schaefer 2002). Although such studies have improved our understanding of predator–prey interactions, whether their findings can be generalized to more complex trophic interactions remain a challenge for future research (Kratina, Vos & Anholt 2007), and particularly in the context of rapid environmental changes. The current theoretical framework on predator–prey interactions is mostly based on specialist predators, and theoretical predictions about how generalist predators should respond to changes in their prey community are unclear. Little is known as yet about how the composition of a prey community influences the dynamics of generalist predators, despite generalist predators constituting an important part of the predator communities. Simultaneously, the shape of numerical and functional responses of predators can have dramatic repercussions for prey community stability and composition, with generalist predation expected to either stabilize (Erlinge *et al.* 1988; Henke & Bryant 1999) or destabilize the community (Holt 1977; Bonsall & Hassell 1997), depending on ecological conditions.

Generalist predators, or predators relying on several prey species in one particular locality, are theoretically expected to maintain relatively constant vital rates, and therefore to display more stable population dynamics both in space and time, compared with specialist predators, due to their ability to switch between alternative species within their prey spectrum (Erlinge *et al.* 1984; Redpath & Thirgood 1997). A generalist predator might be affected by changes in diversity, total biomass and composition of communities at lower trophic levels. Changes in relative species abundance within the prey community are therefore expected to have carry-over effects on changes at higher trophic levels and also possibly to alter interactions among species. These statements, however, remain largely theoretical as empirical studies of the population dynamics of generalist predators have so far encountered difficulties in collecting rigorous data on variation in density for an entire community of prey (for such exceptional studies, see Redpath & Thirgood 1999; Prugh 2005; Rutz & Bijlsma 2006).

Here, we investigate the growth rate of a population of European sparrowhawk *Accipiter nisus* L. during a long-term study that encompassed changes in prey community composition. This small raptor is one of the commonest avian predators in the Western Palearctic, and is portrayed as a prototypical generalist predator, preying on a large variety of passerine birds weighing < 250 g (the five commonest prey species typically represent ≤50% of the diet; Newton 1986), mainly. Our study took place in an open farmland landscape in Northern Denmark and was based on a large data set on dietary regime and population size of the sparrowhawk collected over 20 years (Nielsen 2004a, b; Nielsen & Møller 2006). Furthermore, we took advantage of a national breeding bird survey to investigate population trends of species constituting the prey spectrum of sparrowhawks. The bird community inhabiting farmland in particular is known to have been subject to drastic changes as a consequence of, among other things, intensified agricultural practices across Europe during recent decades (Krebs *et al.* 1999; Donald, Green & Heath 2001; Newton 2004). Therefore, the composition of the avian community was expected to have changed markedly in the study area (Møller 1983a, 2001), thus providing a unique opportunity to investigate the mechanisms underpinning population dynamics of a generalist predator such as the sparrowhawk. The specific objectives of this study were to determine (1) changes in the composition of the prey community by analysing temporal trends within the prey community of the sparrowhawk, (2) the extent of the dietary shift achieved by this generalist predator, (3) how these changes resonate into the dynamics of the sparrowhawk population and, lastly, (4) the demographic processes involved.

Materials and methods

STUDY AREA AND PREDATOR CENSUS

JTN studied European sparrowhawks in an area of 2417 km² around Sindal (57°28′ N, 10°10′ E), Northern Jutland, Denmark (Nielsen & Møller 2006). The study site is a rural area of mixed open farmland with scattered forests, connected by a network of hedges. Woodland covers on average only 4% of this core area allowing a thorough survey of sparrowhawk territories to be conducted. Two adjacent sites within the study area constituted the core of the study (Sindal: 68 km², West of Hjørring: 436 km²), in which sparrowhawk breeding density was accurately recorded between 1978 and 1997 ($n = 930$ nesting attempts summed over all years; Nielsen & Møller 2006). JTN visited all possible breeding sites one to five times annually during the breeding period, searching the forests for sparrowhawk nests. The minimum requirement to consider a territory as occupied was the record of a new nest in a territory or the presence of a pair during the breeding season (see also Newton 1986). Sparrowhawk density averaged ($\pm$SD) 9·3 $\pm$ 1·6 occupied territories per 100 km².

Breeding females were identified and aged (1 year old vs. older) from characteristics of moulted primary feathers found near the nest, using the criteria reported by Opdam & Müskens (1976; see also Newton 1986; Nielsen 2004a). We used territory turnover as a proxy for investigating variation in the apparent survival of breeding females. A female that disappeared from a territory can be considered to be dead with a high probability, as only 5·7% of the females changed territory between years in the study area (Nielsen 2005). On average, 58·1% of breeding females were found for 2 successive years in the same territory which, added to 5·7% of females found in another territory, provides a minimum figure of 63·8% for annual survival. This estimate is very close to the annual survival rate estimated for sparrowhawks (*c.* 66%; Newton 1986). Estimates of the proportion of yearling females in the population and female turnover were available for 18 and 16 years respectively. No such data were available for males.

We obtained mean monthly temperatures from the meteorological stations at Hjørring and Tylstrup (southern edge of the study area). Average daily temperature was calculated for the three coldest months in winter (December–February), as well as for the early spring (February–April), assuming that these periods were the most critical for sparrowhawks. Results are shown only with the period that provided the best fit.

PREDATOR DIET

The diet of the predator during the breeding season was analysed on the basis of prey remains collected, and removed to avoid double counting, near 1709 sparrowhawk nests from the whole study area during April–September 1978–1997, except for 1987 (Nielsen 2004b). A total of 34 923 items were collected of which 34 693 were birds (99·3%, 93 species identified). The number of prey items collected annually averaged 1735 ± 913 (SD; range: 774–3445). A total of 834 prey items remained unidentified at the species level, mainly consisting of undetermined warbler species (*Phylloscopus collybita* Vieill./*trochilus* L., n = 249; *Sylvia communis* Lath./*curruca* L., n = 425). These latter prey items did not contribute substantially to the diet of the sparrowhawk in any year, and they never reached the top-10 in terms of prey species abundance ranking. The contribution of different prey species to biomass ingested by sparrowhawks was calculated by using body mass from Snow & Perrins (1998), averaging values from the two sexes when available. We fixed a maximum threshold of 500 g for any prey species, because sparrowhawks seldom kill heavier prey (Newton 1986). We did not correct for potential predation bias according to sex or age of prey (as data were not available for all prey species), although we acknowledge such a bias has already been documented for some prey species of the sparrowhawk (e.g. Post & Götmark 2006a), including in the present study area (Nielsen 2004b). It is, however, unlikely such a bias would have strongly affected the results, as none of the species considered hereafter (Table 1) is strongly dimorphic in terms of body mass.

Table 1 summarizes the contribution of the 10 most abundant prey species in sparrowhawk diet. The most frequently captured prey species was the skylark *Alauda arvensis* L. with an average frequency of 13·8%, and overall eight species each contributed more than 5%. Other important prey species included the tree sparrow *Passer montanus* L., blackbird *Turdus merula* L., chaffinch *Fringilla coelebs* L., yellowhammer *Emberiza citrinella* L., barn swallow *Hirundo rustica* L., house sparrow *Passer domesticus* L., great tit *Parus major* L., song thrush *Turdus philomelos* L. and starling *Sturnus vulgaris* L. This prey community represented respectively 72·8% and 72·4% of the total abundance and biomass in sparrowhawk diet. Its composition was consistent across the study period as only four other species entered the annual top-10 list during 19 years (white wagtail *Motacilla alba* L., in 7 years; linnet *Carduelis cannabina* L., in 6 years; greenfinch *Carduelis chloris* L. and fieldfare *Turdus pilaris* L., in 1 year each, mostly between ranks 8 and 10). The largest biomass contribution to the sparrowhawk diet (18·9%) was the blackbird (rank 3 in abundance), followed by the skylark (12·5%), with six other species contributing more than 5%. Three larger species contributed disproportionately to prey biomass compared with their abundance in the diet: European jay *Garrulus glandarius* L. (rank 18 in abundance/rank 10 in biomass), fieldfare (16/11) and woodpigeon *Columba palumbus* L. (28/7).

DENSITIES AND TRENDS IN PREY COMMUNITY

Systematic point counts carried out by a network of amateur ornithologists throughout Denmark provided reliable indices of between-year variation in breeding bird densities (Møller 1983b; Grell 1998; Bibby *et al.* 2000). Standard point counts consist of counts of all birds seen or heard at a fixed point during a 5-min period during May–June. We estimated the mean breeding densities for the 10 most abundant species in sparrowhawk diet based on counts recorded in the study area (Møller & Nielsen 2006). We then calculated an index of available biomass each year for each species by multiplying the local mean density by the yearly abundance index estimated at the national level. Abundance indices estimated at the national level (fixed at 100 in 1976, the first year of the national census) for the main prey species of the sparrowhawk were also used to investigate to what extent predator diet varies according to prey abundance. As the study area represents a substantial part of the total area of Denmark (5·5%), yearly variation in abundance of passerines within our study area is assumed to closely match those estimated at the national level. This has been checked for six species for which variation in abundance, assessed independently by APM within the study area, were closely related to those estimated from the breeding bird survey at the national level (barn swallow, r = 0·70, P < 0·0001, n = 28 years; house martin *Delichon urbica* L., r = 0·67, P = 0·0045, n = 16; white wagtail, r = 0·51, P = 0·0047, n = 29; great tit, r = 0·96, P < 0·001, n = 10; starling, r = 0·59, P = 0·0023, n = 24; corn bunting *Miliaria calandra* L., r = 0·78, P = 0·008, n = 10).

Table 1. Population trends and contribution in diet, in terms of abundance and biomass, of the 10 most abundant prey species of the sparrowhawk

Prey species	Population trend Coefficient	Contribution in sparrowhawk diet Abundance %	Biomass %	Rank in biomass
Skylark	−0·04 (0·23)	13·8 (5·2–22·2)	12·5 (4·7–18·2)	2
Tree sparrow	+ 4·01 (1·12)**	11·8 (3·9–21·9)	6·6 (2·1–13·6)	5
Blackbird	+ 2·22 (0·27)***	7·7 (3·6–10·7)	18·9 (8·6–24·1)	1
Chaffinch	+ 1·28 (0·27)***	7·1 (5·7–10·2)	4·0 (3·1–5·8)	9
Yellowhammer	−1·64 (0·22)***	6·7 (4·8–7·6)	4·9 (3·8–6·1)	6
Barn swallow	−0·52 (0·42)	5·9 (1·9–11·4)	2·7 (0·9–5·5)	12
House sparrow	−0·70 (0·28)*	5·6 (2·7–7·4)	4·1 (1·9–6·2)	8
Great tit	−1·13 (0·32)**	5·5 (3·2–7·6)	2·4 (1·3–3·6)	13
Song thrush	−1·14 (0·43)*	4·9 (2·8–7·0)	9·6 (5·7–13·9)	3
Starling	−1·25 (0·53)*	3·8 (2·5–5·4)	6·7 (4·6–9·8)	4

Prey species are ranked by importance according to their abundance in diet. Coefficients (± SE) are taken from a linear regression of the index of abundance for each prey species assessed by the Danish breeding bird survey between 1978 and 1997. The range of annual values are given into brackets for the abundance and the biomass contribution in the sparrowhawk diet.
***P < 0·001; **P < 0·01; *P < 0·05.

STATISTICAL ANALYSES

We evaluated the impact of prey abundance on the growth rate $(\ln[N_t/N_{t-1}])$ of the sparrowhawk population, in interaction with sparrowhawk density (N_{t-1}) and climatic variables. For that purpose, and to assess trends in the main avian prey community, we fitted linear models (LM) with a Gaussian error distribution and an identity link. The information theoretic framework was used for model selection based on Akaike's information criterion corrected for small sample size (AICc, Burnham & Anderson 2002). The relative strength of evidence for each model was assessed using Akaike weights (w_{AICc}), and we used the proportion of variance explained by the model (R^2) as a general measure of goodness-of-fit. We also fitted a piecewise regression with one breakpoint (each year tested as a breakpoint, with the best model being selected with AICc) to test for the occurrence of a two-phase dynamic in the sparrowhawk population trajectory in the core area.

We investigated changes in sparrowhawk diet composition using abundance–biomass–comparison curves (ABC curves), a method initially developed for studies on biodiversity [see Rutz & Bijlsma (2006) for an adaptation of this tool to diet analysis]. For that purpose, prey species were ranked from the most to the least important, and plotted against cumulative contributions in terms of numbers and biomass each year. Curves were subsequently fitted with the equation:

$$f = 1 - e^{-bx}, \qquad \text{(eqn 1)}$$

where f is the cumulative contribution of all prey items (in abundance or in biomass). Equation (1) generates an exponential rise up to a maximum equal to 1, according to a satiation speed represented by b. Increasing values of b signifies a reduction in diet diversity. Variations of prey abundance in the sparrowhawk diet were investigated using generalized linear models with a multinomial error distribution and a logit link using the ratio between the number of a specific prey killed by sparrowhawks and the total number of prey killed as the response variable, with the estimated abundance of prey as the explanatory variable.

Descriptive statistics are presented as mean ± SD and regression slopes as mean ± SE. All statistical analyses were performed using R 2.5.1 (R Development Core Team, 2006).

Results

The number of occupied territories by sparrowhawks in the core area displayed a two-phase dynamic (Fig. 1). The piecewise regression analysis identified two equally likely breakpoints (1989 and 1987, ΔAICc = 0·8), and received a strong support compared with a linear trend (ΔAICc ≥ 9·8). The number of occupied territories decreased from 51 in 1978 to 33 in 1987 (39 in 1989), and recovered afterwards, reaching a maximum of 66 in 1995.

CHANGES IN THE AVIAN PREY COMMUNITY AND VARIATION IN PREDATOR DIET

Among the 10 most abundant prey species in the sparrowhawk diet, eight showed significant temporal linear trends in abundance between 1978 and 1997 (Table 1). The yellowhammer, house sparrow, great tit, song thrush and starling showed significant declines, while tree sparrow, blackbird and chaffinch increased. Changes in the abundance of sky-
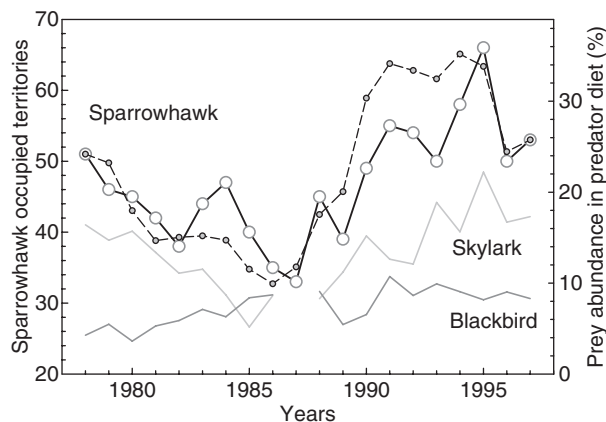

Fig. 1. Temporal dynamics of the sparrowhawk breeding population (number of occupied territories recorded in the core area, open circles). Predicted dynamics by model 6, including previous sparrowhawk numbers (N_{t-1}), index of available biomass of skylarks and blackbirds (in year $t - 1$), and winter temperature (Table 2), is given by the dotted line. The two plain lines refer to the contribution of skylarks (light grey) and blackbirds (dark grey) to the sparrowhawk diet (% of abundance, no data for 1987).
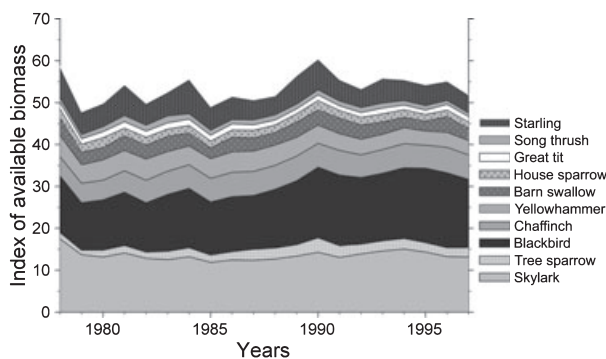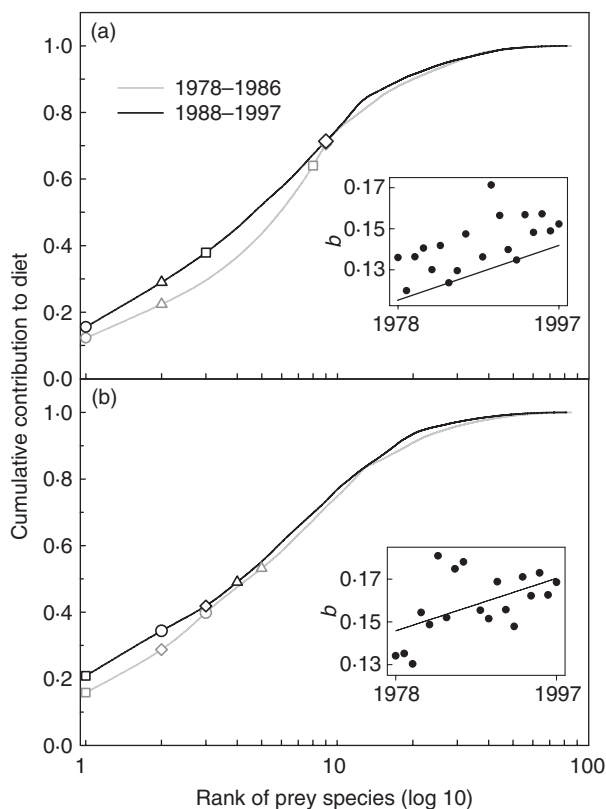

Fig. 2. Cumulative annual variation in available biomass for the 10 most abundant prey species in the sparrowhawk diet (%). Species are ranked from the less frequent (top, starling) to the most common prey (bottom, skylark) for sparrowhawks.

lark and barn swallow were not significant over the study period. However, skylarks decreased in abundance during the first 3 years of the breeding survey (from 100 in 1976 to 82 in 1978). The index of available biomass based on the 10 most abundant prey species did not change throughout the study period (LM; slope: 0·170 ± 0·124, $F_{1,18} = 1·88$, $P = 0·19$; Fig. 2), signifying that the trends of the different species compensated each other. Skylarks and blackbirds, the two most important prey species, represented an increasing proportion of the biomass available for sparrowhawks (between 49·3% and 59·3% annually; slope: 0·306 ± 0·080, $F_{1,18} = 14·7$, $P = 0·0012$; Fig. 2).

For analysing predator diet, we split the data set into two periods: 1979–1986 and 1988–1997 as no data were available for 1987, thus matching one of the two breakpoints identified in the sparrowhawk dynamics. ABC curves differed slightly between the two periods and more so for abundance than for biomass (Fig. 3). The parameter of satiation b (see eqn 1)

Fig. 3. Changes in diet diversity of the sparrowhawk, between the early and late parts of the study using ABC curves, in terms of (a) abundance (average satiation parameter: $b = 0.125 \pm 0.001$, $R^2 = 99.6\%$, and $b = 0.144 \pm 0.001$, $R^2 = 99.4\%$, for respectively 1978–1986 and 1988–1997) and (b) biomass ($b = 0.144 \pm 0.002$, $R^2 = 99.2\%$, and $b = 0.155 \pm 0.002$, $R^2 = 99.2\%$). Skylark (circle), blackbird (square), tree sparrow (triangle) and song thrush (diamonds) are indicated on the curves. Inserted panels indicate the variation of annual satiation parameters during between 1978 and 1997 (no data for 1987).

from these two curves significantly increased over the course of the study period (LM; slope $\times 10^{-3}$: 1.33 ± 0.4, $P = 0.005$; 1.29 ± 0.5, $P = 0.021$ respectively, for abundance and biomass; Fig. 3), revealing a decrease in predator diet diversity. The available biomass of skylark and blackbird combined was positively correlated with the satiation parameter from abundance data ($r = 0.58$, $P = 0.009$), but not with the one from biomass data ($r = 0.16$, $P = 0.51$). This result indicates that sparrowhawk diet diversity decreased as the abundance of its two main prey species increased. In addition, the abundance contribution of blackbird to the sparrowhawk diet almost doubled over the course of the study, leaping from rank 9 to 3 (Fig. 3a), this species thus being the primary source of biomass for sparrowhawks in 17 out of 19 years.

The relative abundance of the different prey species in the predator diet did vary among years (Table 1, Fig. 1). Among the 10 most abundant prey species in sparrowhawk diet, we detected a positive and linear relationship between abundance in diet and density for six species, including the two most important in term of biomass (blackbird and skylark;

Fig. 4). The analysis also retained a significant quadratic term for the house sparrow, implying that satiation in predator seems to have occurred. The levelling off of the relationship, however, as assessed by the maximal fitted value, was only reached for the four highest values of house sparrow abundance.

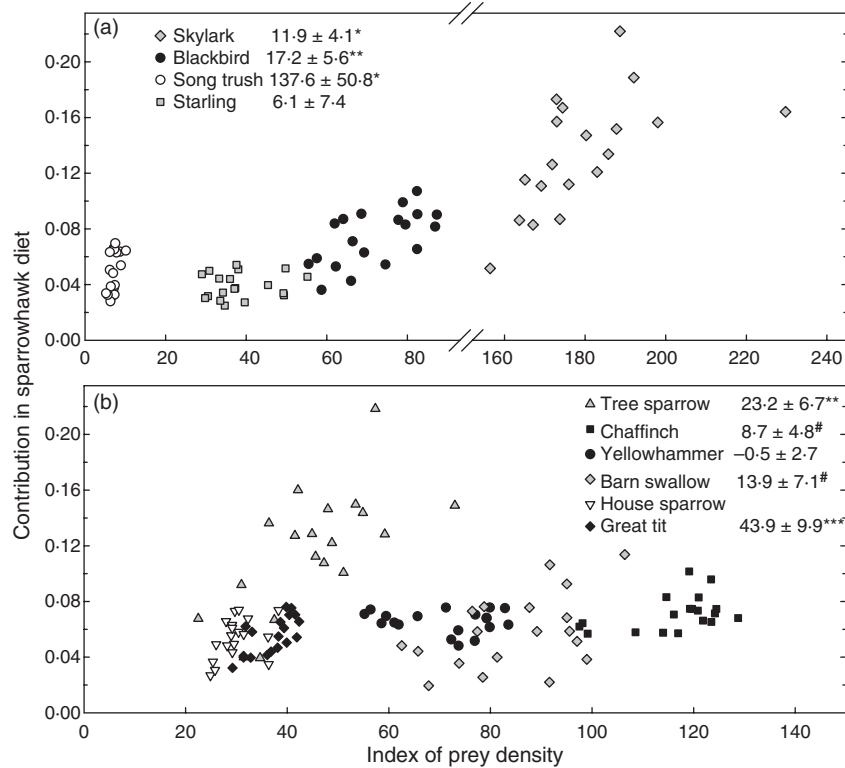### PREDATOR POPULATION DYNAMICS AND DEMOGRAPHIC PROCESSES

We investigated the dynamic of the population of sparrowhawks using multiple regression analyses, and the best supported model retained three terms (model 6 in Table 2). Between-year growth rates in the core area were negatively affected by sparrowhawk density the previous year (direct density dependence). It is noteworthy that the lowest (33 in 1987) and the highest (66 in 1995) numbers of occupied territories were associated with the subsequent highest and lowest values of growth rates respectively (Fig. 1). Adding an index of the prey biomass available in year $t - 1$ sharply increased the explanatory power of the model and the best fit was obtained for an index cumulating the biomass of skylarks and blackbirds. This particular index outperformed those based on a single species, or including the top-10 prey species (compare models 2–5). Finally, cold winters coincided with reductions in the sparrowhawk population growth rate, and the final model that included these three covariates explained 53.1% of the total variance (Table 2). Removing density from this last model considerably reduced the explanatory power (model 7). The results of partial regression analyses from model 6 concerning the effect of population density and prey biomass available are presented in Fig. 5, in contrast with results from raw analyses. Seeded with an initial population size of 51 occupied territories, as recorded in 1978, this model provided a fairly good description of the trajectory of the population (Fig. 1). The main discrepancy between predicted and actual population sizes came from an overestimation of the early increasing phase by the model (growth between 1988 and 1989).

When looking at demographic processes involved, positive growth rates of the sparrowhawk population were positively associated with the recruitment of yearling females (LM; slope $= 1.13 \pm 0.37$, $F_{1,16} = 9.22$, $P = 0.008$, $R^2 = 0.326$; Fig. 6a), but not with the apparent survival of breeding females (slope $= -0.0003 \pm 0.004$, $F_{1,14} = 0.006$, $P = 0.94$; Fig. 6b). This latter parameter was, moreover, almost identical during the decreasing (0.574 ± 0.1, $n = 7$) and the increasing phases (0.587 ± 0.08, $n = 9$) of the sparrowhawk dynamics.

Discussion

PREDATOR DYNAMICS IN A CHANGING ENVIRONMENT

Our analyses revealed the importance of direct density dependence, winter climate and also prey availability in shaping the dynamics of a generalist predator, the Eurasian sparrow-

Fig. 4. Variation in the frequency of occurrence for the 10 most abundant species in sparrowhawk diet according to their density index estimated within the study area. Prey species were grouped according to their body mass as (a) species weighing > 35 g and (b) lighter species. Slopes ($\times 10^{-3} \pm$ SE) are indicated in legend with: $***P < 0.001$; $**P < 0.01$; $*P < 0.05$; $^{\#}P < 0.1$. A best fit was obtained when adding a quadratic term for the house sparrow (density index: $589.1 \pm 209.9*$; quadratic term: $-8.7 \pm 3.2*$).

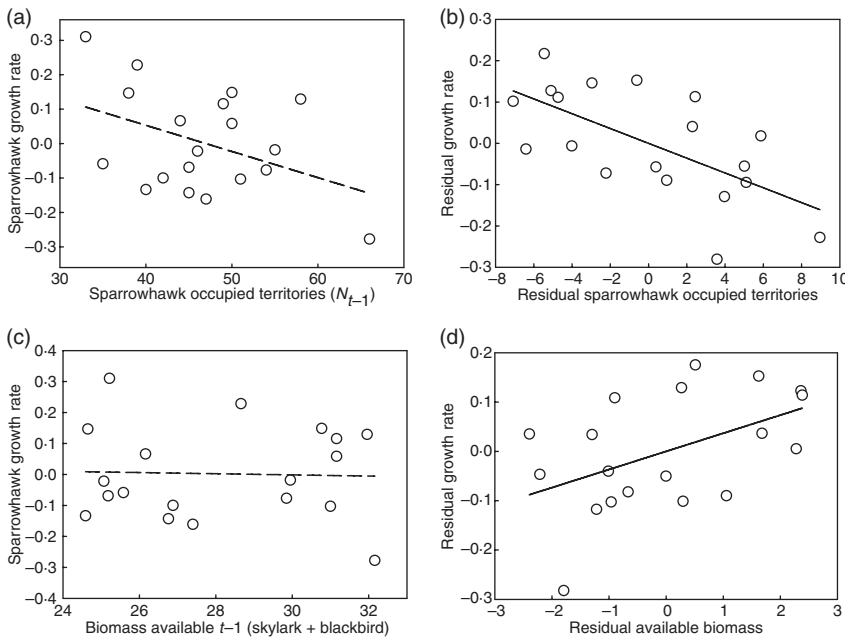**Table 2.** Relative performance of models investigating the population dynamics of sparrowhawk

Sparrowhawk population growth rate, $r = \ln(N_t) - \ln(N_{t-1})$

Model	R^2 (%)	ΔAICc	w_{AICc}
(1) $b_0 + b_1 N_{t-1}$	17·2	5·21	0·029
(2) $b_0 + b_1 N_{t-1} + b_2 \text{Biom}_{10}$	27·0	5·39	0·027
(3) $b_0 + b_1 N_{t-1} + b_2 \text{Biom}_S$	19·1	7·35	0·010
(4) $b_0 + b_1 N_{t-1} + b_2 \text{Biom}_B$	38·2	2·24	0·129
(5) $b_0 + b_1 N_{t-1} + b_2 \text{Biom}_{S/B}$	42·6	0·84	0·260
(6) $b_0 + b_1 N_{t-1} + b_2 \text{Biom}_{S/B} + b_3 T_{\text{winter}}$	**53·1**	**0**	**0·396**
(7) $b_0 + b_1 \text{Biom}_{S/B} + b_2 T_{\text{winter}}$	20·9	6·92	0·012
(8) $b_0 + b_1 N_{t-1} + b_2 T_{\text{winter}}$	38·6	2·12	0·137

The response variable was the inter-annual growth rate calculated as the difference between the ln-transformed numbers of occupied territories (N) in 2 consecutive years. Explanatory variables were previous sparrowhawk density (N_{t-1}), average temperature recorded during the previous winter (December–February, T_{winter}), available biomass of the top-10 prey species (Biom_{10}), and available biomass of respectively skylarks, blackbirds and both species pooled (Biom_S, Biom_B, $\text{Biom}_{S/B}$), in year $t - 1$. Proportion of variance explained by the model (R^2), difference in Akaike Information Criterion corrected for small sample size with the best model (ΔAICc) and AICc weights (w_{AICc}) are presented. The best-supported model is given in bold.
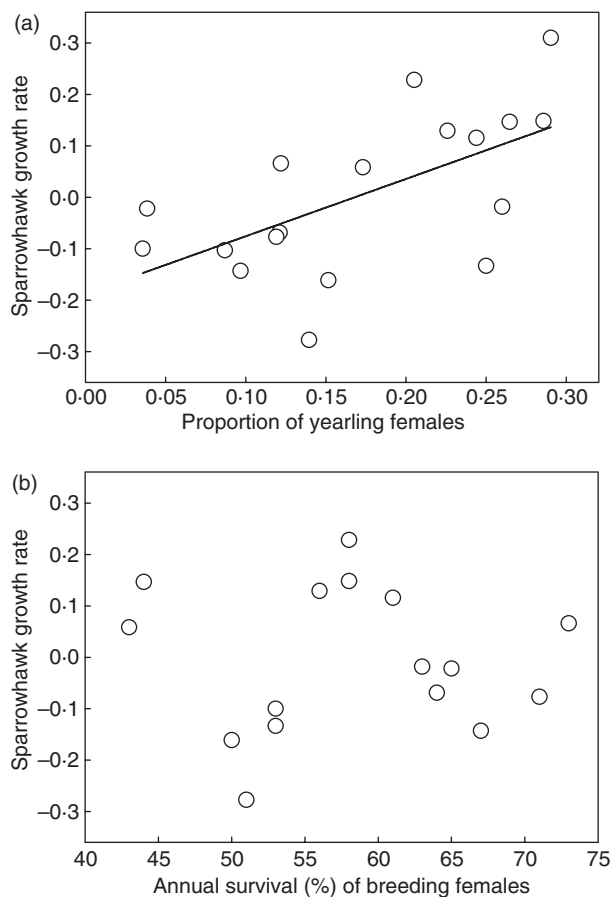
hawk. Changes in the composition of the avian prey community documented here are akin to an unreplicated natural experiment, allowing us to assess the impact of variation in prey abundance on generalist predators. The avian community in the open rural area of Northern Denmark seemed, however, not as critically affected as elsewhere in Europe, as revealed by the comparison of trends in farmland birds between Denmark and the UK (Fox 2004; see also Rutz & Bijlsma 2006). Indeed, the overall prey biomass represented by the 10 favourite prey species of sparrowhawks remained fairly stable during the 20 years of the study (Fig. 2). Nevertheless, change in the composition of the passerine community did occur, with contrasting population trends among prey species. Specifically, the two most important prey species for sparrowhawks in this location, namely the skylark and the blackbird, have experienced distinctive trends. While skylark abundance plummeted in Denmark in the mid-1970s, but then remained stable during the rest of the study period, blackbird abundance displayed a strong increase ($+39\%$ over the course of the study). A similar phenomenon has been described elsewhere in Europe, where populations of typically specialist bird species, especially those inhabiting farming landscape, have collapsed, whereas those of generalist species have concomitantly increased (Voricek 2003). These changes in the relative abundance of passerines in Danish rural areas are most probably attributable to a combined effect of climate warming (Nielsen & Møller 2006), with changes in land use and farming practice (Møller 1983a, 2001; Fox 2004). In addition, predation by sparrowhawks and northern goshawks *Accipiter gentilis* L., may also have contributed to the trends in their prey communities.

These findings extend the insights from a previous study in which Newton (1986) detected a density-independent effect of the weather in spring acting in addition to density-dependent processes, in a less-variable population of sparrowhawks in Scotland (29–39 occupied territories). Two distinct phases were clearly discernible when investigating the population trajectory between 1978 and 1997, with a recovery

Fig. 5. Relationships between the growth rate of the sparrowhawk population, previous sparrowhawk density and available prey biomass, from respectively raw analyses (a and c) and partial regression analyses (b and d), based on the best supported model (model 6, Table 2). For the latter, residuals were taken from a multiple regression of the variable of interest (for both *y*- and *x*-axes) on the two other covariates fitted in the selected model [respectively $biom_{S/B}$ in year $t - 1$ and T_{winter} in (b); N_{t-1} and T_{winter} in (d)]. Lines were drawn from a linear simple regression model, and further indicate whether such models were significant (solid lines) or not (dotted lines).

Fig. 6. Variation in sparrowhawk population growth rates ($r = \ln[N_t] - \ln[N_{t-1}]$) in relation to (a) the proportion of 1-year-old females in the breeding population and (b) the annual apparent survival (%) of breeding females, based on feather identification.

from the mid-1980s following an initial decline (Fig. 1). The analysis of such a trajectory further emphasized the impor-

tance of the availability of particular prey species, in addition to weather conditions and density dependence. The decrease phase until 1987 might be explained by the collapse in skylark abundance in sparrowhawk diet (Fig. 1), combined to the occurrence of three successive harsh winters (from 1984–1985 to 1986–1987). Then, the recovery of the population might have benefited from the increase of both skylark and blackbird in the predator diet.

Using an exceptionally large data set for a generalist predator with information on diet composition, we documented the dynamics of a Eurasian sparrowhawk population in response to changes in its avian prey community. Interestingly and although the analyses included 10 prey species (representing 72% of the total biomass ingested by predators), the growth rate of the sparrowhawk population was mostly linked to variation in the abundance of skylark and blackbird, the two most important species. The dynamics of the blackbird may have compensated for the decline in abundance of the skylark and the song thrush, the two other main sources of biomass for sparrowhawks (Table 2, Figs 2 and 3). While both sparrowhawk males and females prey upon skylarks (*c.* 40 g), heavier prey such as blackbirds (*c.* 100 g) are, however, likely to be caught mainly by females. Male sparrowhawks, however, as with many other raptors, are the almost exclusive food providers to chicks until the second half of the chick-rearing period (Newton 1986). Therefore, blackbirds can certainly not fully substitute for skylarks into sparrowhawk diet during the breeding season, and other small prey species (e.g. the tree sparrow and the chaffinch) might be of importance for sparrowhawks during the laying period.

Our analyses also pointed out the pitfalls inherent in the assumptions of constant carrying capacity within the density-dependence framework (see also Chamaillé-James *et al.* 2008). While raw analyses detected neither direct density

dependence nor an effect of prey abundance on predator growth rates, partial regression analyses revealed that both predator and prey abundance did matter (Millon & Bretagnolle 2008). The effects of both predator numbers (negative) and available prey biomass of the two main prey species (positive) appeared to be linear (Fig. 5). Such findings give some support to the ratio-dependent predation hypothesis (Abrams & Ginzburg 2000), but more investigations of the functional response of generalist predators are certainly needed.

We found support for the recruitment rate of young female sparrowhawks being the main demographic driver of variation in population size (see also Wyllie & Newton 1991). Inter-annual population growth rates were indeed dependent on recruitment of first-year females, but not on apparent survival of breeding females. Three non-mutually exclusive explanations can account for this pattern. First, higher prey abundance in spring may facilitate the recruitment of yearling females, that generally require more profitable conditions to enter the breeding population than older ones (Curio 1983). Second, the increase in blackbird abundance (a resident species) may have reduced the overwinter loss of sparrowhawks, which was previously identified as the key factor underpinning variation in breeding numbers of a resident sparrowhawk population (Newton 1988). This latter hypothesis was, however, not supported by variation in the survival of breeding females, but may rather act primarily on first-year survival and thus ultimately favour recruitment *in fine*. Thirdly, the increasing occurrence of mild winters may also have positively impacted the population, by favouring the survival of sparrowhawks and especially juveniles, these birds being more prone to move away and more susceptible to harsh conditions.

Although the documented change in the avian prey community can be considered as an interesting natural experiment, such an analysis remains correlative, and therefore causation can only be inferred with caution. Nevertheless, several lines of evidence strengthen the above conclusions about the direct impact of changes in the prey community on sparrowhawk dynamics. First, the dynamics of this sparrowhawk population could result from the ban on organochlorine pesticides in 1984, these chemicals being known to have heavily affected avian predators like sparrowhawks (Newton 1986). The usage of organochlorines by farmers was progressively reduced from the end of 1960s (Newton & Wyllie 1992), including in Denmark (Anders Pape Møller, unpublished data), and most sparrowhawk populations throughout Europe were documented to be recovering during the late 1970s, including the most affected population from eastern England (Newton & Haas 1984; Newton & Wyllie 1992). For instance, Opdam, Burgers & Müskens (1987) recorded in the Netherlands that sparrowhawk numbers increased consistently across seven different locations between 1970 and 1982. At the same time, the numbers of sparrowhawk in our study area fell from 51 to 38 pairs between 1978 and 1982 (Fig. 1). Unlike DDT that primarily reduced eggshell thickness, the last generation of cyclodiene organochlorines

(dieldrin and aldrin) killed adult sparrowhawks directly (Newton, Wyllie & Asher 1992). Using territory turnover of breeding females as a proxy, we did not detect any difference in female apparent survival between the two periods. These findings indicate that the recovery from pesticides in Northern Denmark might have occurred before the start of the present study, making the pesticide hypothesis unlikely to be the main causal factor of the observed sparrowhawk dynamics during the period considered.

Second, population dynamics of the sparrowhawk may also have been affected by species at higher trophic levels. In particular, the northern goshawk is suspected to be a key species in intra-guild predation as it regularly kills raptors (Petty *et al*. 2003), including sparrowhawks (Rutz & Bijlsma 2006; Jan Tøttrup Nielsen, unpublished data). In our study area, the goshawk bred at very low density during the 1960s and 1970s (Møller, Sørensen & Sperling 1978), while breeding numbers increased between 1977 and 1997 from 5 to 17 pairs (Nielsen & Møller 2006) in parallel with sparrowhawks. Intra-guild predation and intense interspecific competition with goshawks are therefore unlikely to account for the two-phase dynamic documented here.

INTERACTIONS BETWEEN A GENERALIST PREDATOR AND ITS PREY COMMUNITY

We showed the versatility of the sparrowhawk and especially its ability to adjust its diet composition to the current abundance of a large variety of prey (Figs 1 and 4). Among the 10 most abundant prey species in the sparrowhawk diet, six significant relationships were detected between the index of prey density and contribution to diet, including among the blackbird and the skylark, the two most important prey species in terms of biomass or abundance. The diet width of sparrowhawks in Northern Denmark was comparable with that previously described elsewhere in Europe (review in Newton 1986). Although the prey spectrum remained constant during the study, the changes in prey community composition resulted in a reduction of diet diversity (Fig. 3). The increase in blackbirds seems to be the main factor responsible for this change in predator diet. Predators may, in addition to abundance, select their prey so as to maximize profitability according to prey vulnerability and body mass. Prey vulnerability to predation may differ according to coloration (Møller & Nielsen 2006), behaviour (Götmark & Post 1996; Møller, Nielsen & Erritzøe 2006; Post & Götmark 2006a, b), and parasite load of prey (Møller & Nielsen 2007), or be altered by changes in habitat structure in relation to farming practice (Whittingham & Evans 2004). However, the main changes in habitat structure (abundance and distribution of hedges, ponds, field boundaries and other habitats) mainly occurred during the 1960s and early 1970s, i.e. before the start of the present study (Møller 1983a).

Generalist predators are expected to primarily respond functionally rather than numerically to a change in prey abundance (Andersson & Erlinge 1977). A diverse diet should allow sparrowhawks to buffer variation in the abun-

dance of individual prey species and so maintain relatively stable vital rates in the face of changes in the composition of prey communities. Our results are in line with findings from a study on goshawks in the Netherlands where a drop in goshawk numbers was accompanied by a sharp increase in diet diversity (Rutz & Bijlsma 2006). Petty *et al.* (1995) also documented that sparrowhawks were able to take advantage of an irruption of common crossbills *Loxia curvirostra* L. and siskins *Carduelis spinus* L. following a massive production of spruce cones, by responding both functionally and numerically to a sudden change in the composition of the prey community. These studies, together with our results, suggest rather unexpectedly that, if although they are able to prey upon a large variety of prey, generalist predators such as the European *Accipiter* may actually be highly dependent upon a few species.

Predation is an important force structuring communities, and sparrowhawks may impact the structure of prey communities they exploit. We identified the conditions that may trigger an apparent competition between two thrush species, the blackbird and the song thrush. The song thrush seemed to be highly vulnerable to sparrowhawk predation (see also Bijlsma 1993) as it showed the largest functional response by sparrowhawks (Fig. 4), despite a low-average population density (seven times lower than blackbird density). Predation from sparrowhawks, maintained at high density by blackbirds, may prevent song thrushes from recovering, and hence possibly keeps this species in a predator trap. Consistently, the abundance indices of the two species during the study period were negatively correlated, although only marginally so ($r = -0.43$, $P = 0.056$). Such results are actually concordant with two analyses conducted in the UK at different spatial scales, which identified the song thrush as the most vulnerable species to sparrowhawk predation among songbirds (Newton, Dale & Rothery 1997; Thomson *et al.* 1998), although factors other than predation, such as land use, might also contribute to the dynamics of the song thrush (Robinson *et al.* 2004).

Ultimately, our analyses of extensive long-term data sets on prey availability, diet composition and population dynamics of the Eurasian sparrowhawk revealed that relatively subtle changes in the community of prey can affect predator dynamics. This in turn may have implications for the trophic cascade and lead to a re-organization of a wider community. Assessing the impact of contemporary changes in terms of climate or land use on species interactions within a trophic network, rather than focusing on single-species dynamics, appears therefore an important challenge for ecologists.

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